RHINOLOPHOIDEA (CHIROPTERA, MAMMALIA) FROM THE UPPER OLIGOCENE OF CARRASCOSA DEL CAMPO (CENTRAL SPAIN)

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ABSTRACT

For the first time in Spain, an Oligocene bat fauna is described from the alluvial locality of Carrascosa del Campo. Four species are present: two belong to *Hipposideros (Pseudorhinolophus)* another to *Rhinolophus* and a fourth one to *Megaderma*. Three new species are described : *Hipposideros (Pseudorhinolophus) minor* nov. sp., *Hipposideros (Pseudorhinolophus) conquensis* nov. sp. and *Megaderma lopezae* nov. sp.. *Hipposideros (Ps.) minor* nov. sp. is closely related to *Hipposideros (Ps.) morloti* (PICTET) and *Hipposideros (Ps.) conquensis* nov. sp. to *Hipposideros (Ps.) schlosseri* (REVILLIOD). *Megaderma lopezae* nov. sp. is the smallest species of the genus *Megaderma*. *Rhinolophus* sp. belongs to the *R. hipposideros* size group, and might be related to *R. priscus* REVILLIOD.

RHINOLOPHOIDEA (CHIROPTERA, MAMMALIA) DE L'OLIGOCÈNE SUPÉRIEUR DE CARRASCOSA DEL CAMPO (ESPAGNE CENTRALE).

RÉSUMÉ

Une faune de chiroptères oligocènes est décrite, pour la première fois en Espagne, provenant du gisement alluvial de Carrascosa del Campo. Il y a quatre espèces présentes, dont deux appartiennent au genre *Hipposideros (Pseudorhinolophus),* une autre au genre *Rhinolophus* et une quatrième au genre *Megaderma.* Trois espèces nouvelles sont définies : *Hipposideros (Pseudorhinolophus) conquensis* nov. sp., *Hipposideros (Pseudorhinolophus) minor* nov. sp. et *Megaderma lopezae* nov. sp.. *Hipposideros (Ps.) minor* nov. sp. est proche d'*Hipposideros (Ps.) morloti* (PICTET) et *Hipposideros (Ps.) conquensis* nov. sp. d'*Hipposideros (Ps.) schlosseri* (REVILLIOD). *Megaderma lopezae* nov. sp. est la plus petite espèce décrite jusqu'à maintenant appartenant au genre *Megaderma. Rhinolophus* sp. pourrait être en relation avec *R. priscus* REVILLIOD.

KEY-WORDS : CHIROPTERA, HIPPOSIDEROS (PSEUDORIHNOLOPHUS), RHINOLOPHUS, MEGADERMA, UPPER OLIGOCENE, CENTRAL SPAIN.

MOTS-CLÉS : CHIROPTERA, HIPPOSIDEROS (PSEUDORHINOLOPHUS), RHINOLOPHUS, MEGADERMA, OLIGOCÈNE SUPÉRIEUR, ESPAGNE CENTRALE.

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RESUMEN

Se describe por vez primera una fauna de quirópteros oligocenos de España, perteneciente al yacimiento aluvial de Carrascosa del Campo. De las cuatro especies presentes, dos pertenecen al género *Hipposideros (Pseudorhinolophus)*, otra al género *Rhinolophus* y una cuarta al género *Megaderma*. Se definen tres nuevas especies : *Hipposideros (Pseudorhinolophus) conquensis* nov. sp., *Hipposideros (Pseudorhinolophus) minor* nov. sp., *Megaderma lopezae* nov. sp.. *Hipposideros (Ps.) minor* nov. sp. es próximo a *Hipposideros (Ps.) morloti* (PICTET) e *Hipposideros (Ps.) conquensis* nov. sp. a *Hipposideros (Ps.) schlosseri* (REVILLIOD). *Megaderma lopezae* nov. sp. es la especie de *Megaderma* de menor talla descrita hasta el momento. *Rhinolophus* sp. podría estar relationado con *R. priscus* REVILLIOD.

INTRODUCTION

Carrascosa del Campo is an upper Oligocene locality in the province of Cuenca (Central Spain). This locality was first described by Crusafont & Aguirre (1973). Vilas-Minondo and Pérez-Gonzàlez (1971) place the locality at the base of the stratigraphical unit, which presently bears the name of the Upper Detritic Unit (Diaz-Molina 1974a). In the same paper, Diaz-Molina rectifies the stratigraphical position of the locality and places it at the top of the Lower Detritic Unit. Diaz-Molina *et al.* (1985, fig. 2) rectify its position for a second time and assign it to the Upper Detritic Unit again, but consider it to occupy a higher place than originally assigned by Vilas-Minondo and Pérez-González (1971).

The sediments of the locality of Carrascosa are now considered to be of local provenance. They include reworked materials from the underlying Lower Detritic Unit, and are contemporaneous with the tectonical deformation causing the anticlinal structure of Carrascosa del Campo (Diaz-Molina, pers. comm.). More details of the geology of the basin and of the locality can be found in Díaz-Molina (1974b) and in Díaz-Molina & López-Martinez (1979).

From 1983 onwards, Carrascosa has been systematically excavated, and a large number of mammal remains have been obtained. This material is described in Daams, Lacomba & López-Martínez (1986), Lacomba & Morales (1987) and in Lacomba (1988). Large Mammals are represented, among others, by *Metriotherium mirabile* (FILHOL) and *Eggysodon osborni* (SCHLOSSER). Only five rodent species have been described, including *Issiodoromys minor* (SCHLOSSER), *Archaeomys gracilis* (SCHLOSSER), *Pseudocricetodon incertus* (SCHLOSSER) and *Gliravus alvarezae* LACOMBA & MORALES. The age of the locality is fixed in Arvernian, upper Oligocene and within Unit T of the local biozonation (Alvarez-Sierra *et al.*, 1987). Unit T has been correlated to the French locality of Rigal-Jouet, and is therefore situated in MP25 of the European Mammal biochronological standard level (Schmidt-Kittler, 1987).

Among the micromammal remains, a large proportion belong to bats (42%). From the point of view of this fauna, Carrascosa del Campo is a very interesting locality for sevaral reasons. On the one hand it is one of the few alluvial localities in Europe with abundant bat fauna. The majority of the localities of this age in Europe with bat remains are of karstic nature (see Sigé & Legendre 1983). The high proportion of bat remains in relation to the rodents found in Carrascosa is quite uncommon, as in fluvial localities the rodent fauna is generally accompanied by few bat remains. This fact allowed to propose a hypothesis referring to the origin of the locality.

MATERIAL AND METHODS

As most frequently happens in the Spanish fossil localities with bat remains, these consist basically of isolated teeth. A few mandible fragments carrying one or two teeth, but without mandibular ramus, are found in the Carrascosa material. This makes it difficult to identify the material correctly, especially when we try to arrive at the species level. Nevertheless, the presence of a high number of remains in Carrascosa compensates this lack of information, and it makes it possible to recognize and describe four species, of which three are new.

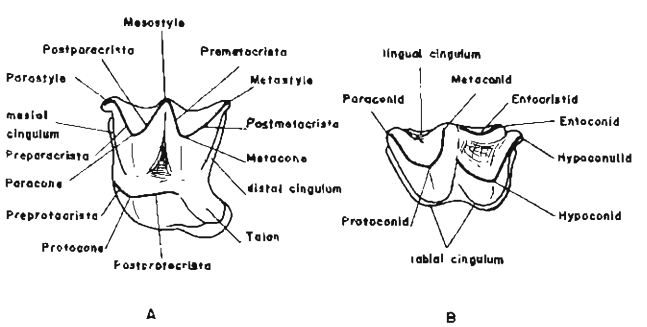

Figure 1 - Nomenclature used for the description of the upper (A) and lower (B) molars. (after Van Valen (1966) and Menú & Sigé (1971)).

Nomenclature utilisée pour la description des molaires supérieures (A) et inférieures (B). (d'après Van Valen (1966) et Menú et Sigé (1971)).

The criteria which have been used for identification and description of the material are described in Sevilla (1986) and Sevilla & López-Martínez (1988). The nomenclature of parts of the teeth is after Van Valen

(1966) and Menú & sigé (1971) (figure 1) and that of the humera after Felten, Helfricht & Storch (1973). Measurements were taken following Sigé (1968) and Sevilla (1986), except for the width of the upper molars, which was measured as shown in figure 2. The specimens described in this work are stored in the collections of the Department of Paleontology of the Universidad Complutense of Madrid.

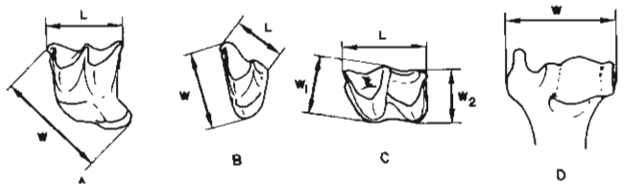

Figure 2 - Measurements taken in the upper molars (A and B), lower molars (C) and distal epiphysis of the humera (D).

Mesures pris sur les molaires supérieures (A et B), les molaires inférieures (C) et les épiphyses des humérus (D).

SYSTEMATIC DESCRIPTIONS

Family HIPPOSIDERIDAE Miller 1907
Genus *Hipposideros* GRAY, 1831
Subgenus *Pseudorhinolophus* SCHLOSSER, 1887

HIPPOSIDEROS (PSEUDORHINOLOPHUS) MINOR NOV. SP.

Holotype - Left M^1, CAS-152 (fig. 7 ; 2).

Hypodigm - Isolated teeth, CAS-032, -092, -178, -201, -229, -245, -283, -312, -423, -462, (fig. 7 : 1, 3-6 ; fig. 8 : 1-4 ; fig. 9 : 1).

Type locality - Carrascosa del Campo (province of Cuenca, Spain).

Distribution - MP25, upper Oligocene, Central Spain.

Diagnosis - Small *Pseudorhinolophus* species. Postprotocrista of upper molars directed towards the base of the metacone, but separated from it by a narrow valley. The third upper molar presents a strong distal reduction ; the premetacrista of this tooth measures about one half of the length of the postparacrista. The preprotocrista of M^3 leans on the base of the paracone and does not join the mesial cingulum. The height of the mandible is uniform from P_4 to M_3 but decreases just behind the latter tooth. Humera with short and rounded styloid process.

Differential diagnosis - Of similar size as *H. morloti* (PICTET), slightly larger than *H. trassounius* SIGÉ and somewhat smaller than *H. schlosseri* (REVILLIOD). The height of the mandible is constant from the P_2 to the end of the M_2, and starts to decrease below M_3 in *H. minor* nov. sp. In both *H. morloti* as in *H. schlosseri*, the maximal height of the mandible is at the M_3. The mandibular symphysis in *H. minor* nov. sp. protrudes ventrally, whereas in *H. morloti* it is evenly rounded. Talonids of the lower molars in *H. minor* nov. sp. proportionatelly longer than in *H. shlosseri* and *H. trassounius*. Talon of P^4, M^1, M^2 and parastyle in upper molars less developed than in *H. trassounius*. The styloid process of the humera is shorter than in *H. schlosseri*.

Measurements - see Table 1.

		n	$\bar{x}$	min. - max.	σ n-1	Σx^2
C*	L	62	1,44	1,37 - 1,52	0,04	130,26
	W	64	0,92	0,78 - 1,09	0,06	55,57
P4	L	13	0,99	0,90 - 1,05	0,05	12,70
	W	4	1,15	1,13 - 1,21	-	-
M^1	L	27	1,49	1,37 - 1,56	0,04	60,76
	W	32	2,05	1,94 - 2,23	0,07	135,68
M^2	L	19	1,44	1,37 - 1,52	0,04	39,77
	W	25	1,97	1,84 - 2,07	0,06	97,19
M^3	L	27	0,99	0,92 - 1,05	0,02	26,52
	W	28	1,47	1,37 - 1,52	0,03	60,53
C.	L	53	0,78	0,70 - 0,90	0,04	32,50
	W	56	0,78	0,68 - 0,90	0,05	34,81
P_2	L	1	0,74	-	-	-
	W	1	0,58	-	-	-
P_4	L	28	0,9	0,86 - 0,98	0,03	23,18
	W	27	0,74	0,70 - 0,88	0,03	15,20
M_1	L	38	1,49	1,33 - 1,78	0,06	84,88
	W_1	42	0,82	0,74 - 0,94	0,04	28,38
	W_2	39	0,90	0,86 - 0,98	0,03	31,64
M_2	L	46	1,46	1,37 - 1,56	0,04	99,19
	W_1	49	0,87	0,78 - 0,98	0,04	37,66
	W_2	48	0,91	0,82 - 0,98	0,03	40,58
M_3	L	27	1,31	1,21 - 1,41	0,04	46,43
	W_1	27	0,84	0,78 - 0,94	0,03	19,53
	W_2	29	0,61	0,54 - 0,74	0,03	11,11
H	W	6	3,06	2,94 - 3,21	0,12	56,50

Table 1 - Measurements in mm of the teeth of ***Hipposideros (Pseudorhinolophus) minor*** nov. sp. from Carrascosa del Campo.

*Mesures en mm des dents d'**Hipposideros (Pseudorhinolophus) minor** nov. sp. de Carrascosa del Campo.*

Derivatio nominis - *minor* - after its relatively small size.

Material - 66 upper canines, 13 P^4, 33 M^1, 26 M^2, 28 M^3, 56 lower canines, 1 P_2, 28 P_4, 42 M_1, 50 M_2, 30 M_3, 6 humera.

Description - Upper canine : Long, with a well-developed lingual cingulum. Labially the cingulum is absent. The tooth wear at the posterior edge of the crown reaches the cingulum. In occlusal view, the outline varies from semicircular to triangular, as a consequence of the considerable variation observed in the development of the talon (figure 3). The lingual cingulum is unevenly concave, marking an angulosity at the distal half.

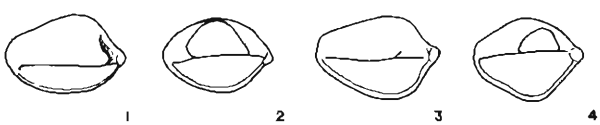

Figure 3 - Variability in the development of the talon of the upper canines of ***Hipposideros (Pseudorhinolophus) minor*** nov. sp.

Variabilité dans le développement du talon des canines superieures d'Hipposideros (Pseudorhinolophus) minor nov. sp.

P^4 : this tooth is provided of a well developed talon and the concavity which marks its beginning at the distal margin varies from evenly rounded to angular (see figure 4). The cingulum presents an anterolingual cusplet located beside the base of the protocone. At the anterolabial side of the crown the cingulum is wider, but no cingular cusplet is present.

Figure 4 - Variability in the development of the talon of the P^4 of ***Hipposideros (Pseudorhinolophus) minor*** nov. sp,

Variabilité dans le développement du talon de P4 d'Hipposideros (Pseudorhinolophus) minor *nov. sp.*

M^1 : this tooth presents a subquadrate outline in occlusal view. The anterior cingulum starts at a small distance from the parastyle, where it widens slightly. It connects lingually to the preprotocrista. The postprotocrista runs parallel to the lingual margin, and disappears without joining either the distal cingulum or the talon cingulum. A well developed talon is present, variable in size and shape (see fig. 5) and without hypocone. The cingulum of the talon, connected with the distal cingulum, ends at its anterior edge at the base of the protocone.

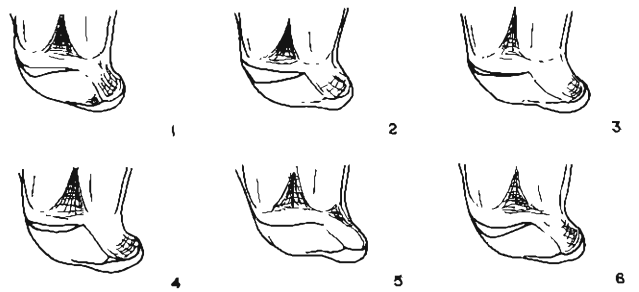

Figure 5 - Variability in the development of the talon of the M^1 of ***Hipposideros (Pseudorhinolophus) minor*** nov. sp.

Variabilité dans le développement du talon de M^1 d'Hipposideros (Pseudorhinolophus) minor nov. sp.

M^2 : it has a rectangular outline, and resembles the M^1, except for the smaller talon, which presents a stronger variability in size and shape (fig. 6). The postprotocrista runs obliquely towards the distal cingulum at the lingual margin, but without joining it.

M^3 : the distal reduction of this tooth is strong. Metastyle and postmetacrista are absent ; the metacone is present, and its anterior crest, the premetacrista, is strongly reduced to about one half the length of the

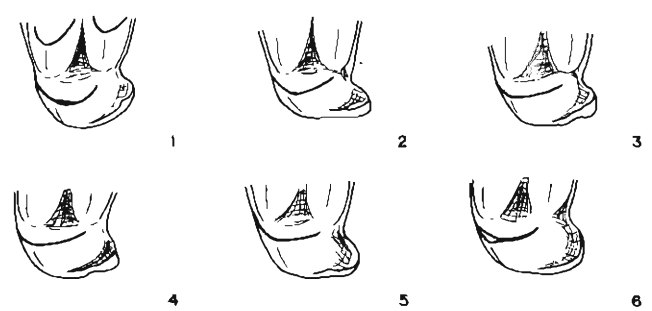

Figure 6 - Variability in the development of the talon of the M^2 of ***Hipposideros (Pseudorhinolophus) minor*** nov. sp.

Variabilité dans le développement du talon de M^2 d'Hipposideros (Pseudorhinolophus) minor nov. sp.

postparacrista. The postparacrista is only slightly reduced. There is an isolated mesial cingulum, that does not join the preprotocrista. It runs from the base of the parastyle and ends at the mesial base of the protocone. The preprotocrista starts at the lingual base of the paracone and does not join the mesial cingulum.

Lower canine : Trapezoidal outline in occlusal view. The cingulum is continuous around the tooth and thin at the labial side. It has two cusplets, of which one is situated at the mesial side and the other at the posterolingual side. Lingually, the crown presents a swelling

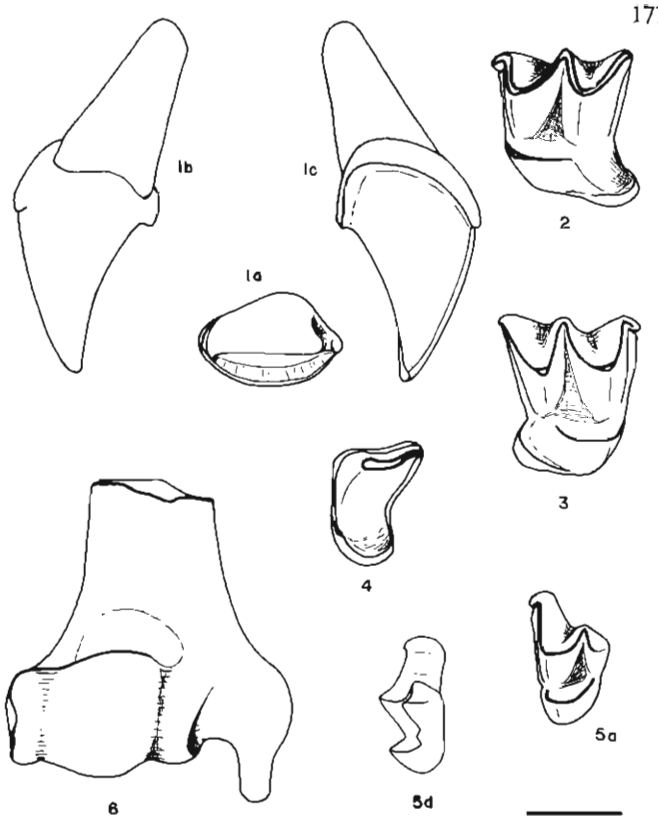

Figure 7 - ***Hipposideros (Pseudorhinolophus) minor*** nov. sp. 1 : left upper canine (CAS-32-Q). 2 : holotype, left M^1 (CAS-152-Q). 3 : right M^2 (CAS-178-Q). 4 : left P^4 (CAS-462-Q). 5 : left M^3 (CAS-201-Q). 6 : distal epiphysis of right humerus (CAS-312-Q). (a : occlusal ; b : labial ; c : lingual ; d : distal. The scale = 1 mm).

1 : Canine supérieure gauche (CAS-32-Q). 2 : holotype, M^1 gauche (CAS-152-Q). 3 : M^2 droite (CAS-178-Q). 4 : P^4 gauche (CAS-462-Q). 5 : M^3 gauche (CAS-201-Q). 6 : épiphyse distale de l'humérus droit (CAS-312-Q). (a : occlusale ; b : labiale ; c : linguale ; d : distale. Echelle = 1 mm).

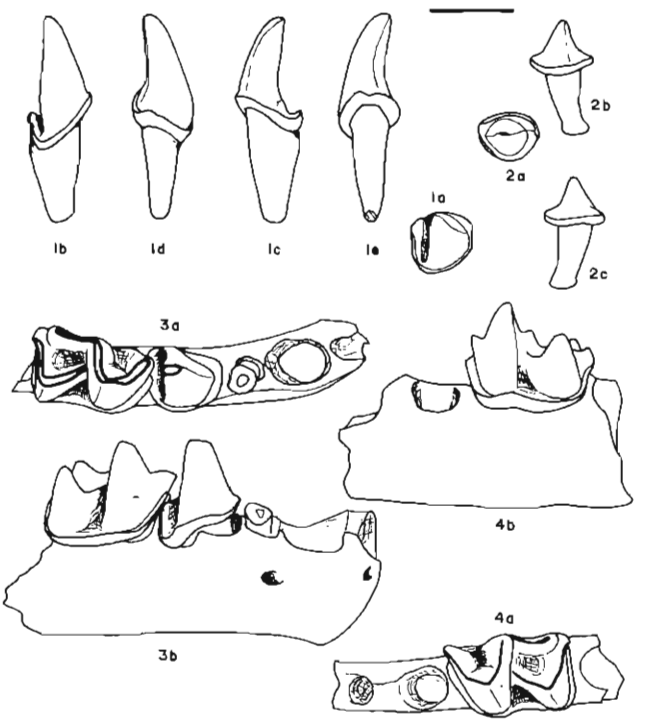

Figure 8 - ***Hipposideros (Pseudorhinolophus) minor*** nov. sp. 1 : right lower canine (CAS-92-Q). 2 : left P_2 (CAS-423-Q). 3 : fragment of right mandible with P_4 and M_1 (CAS-229-Q). 4 : fragment of left mandible with M_2 (CAS-245-Q). (a : occlusal ; b : labial ; c : lingual; d : distal ; e : mesial. The scale = 1 mm).

1 : Canine inférieure droite (CAS-92-Q). 2 : P_2 gauche (CAS-423-Q). 3 : fragment de mandibule gauche avec P_4 et M_1 (CAS-229-Q). 4 : fragment de mandibule gauche avec M_2 (CAS-245-Q). (a : occlusale ; b : labiale ; c : linguale; d : distale ; e : mésiale. Echelle = 1 mm).

in its base. This tooth is provided of a strong root which is longer than wide.

P_2 : this tooth presents an oval outline in occlusal view; the single cusp is somewhat displaced towards the lingual margin of the tooth. The height of the crown at the labial side is about the same as at the lingual side. There is a continuous cingulum all around the base of the crown. The single root is strong and its tip is slightly swollen and bent distally.

P_4 : it has a subrectangular outline, and it presents one main cusp which is situated at the centre of the crown. The cusp has three faces, the one at the lingual side presents a swelling at the base. From a labial point of view, the cingulum runs horizontally up to the end of the mesial root, where it starts to run downwards. Two cingular cusplets are present, one at the mesiolingual side, the other at the distolingual one. Two roots are present.

M_1 : with a long and narrow trigonid. The talonid, which is wider than the trigonid, presents a well-developed hypoconulid standing wide apart from the entoconid and at a more labial position than the other lingual cusps. The entocristid is slightly convex towards the lingual side. The tallest cusp is the protoconid, followed by the hypoconid and metaconid. The paraconid and entoconid are similar in height and slightly shorter than the two former cusps. The labial cingulum starts at the base of the paraconid and runs without interruption up to the base of the hypoconulid. Its width is not uniform, becoming thicker between the trigonid and the talonid. There is a small lingual cingulum at the trigonid.

M_2 : this tooth resembles M_1 strongly, but it has a narrower trigonid, as the paraconid and metaconid are standing closer. The rest of the morphology is similar to the first molar.

M_3 : with a wider trigonid than talonid. The width of the talonid is only slightly reduced. The entoconid is located more labially than in the two previous molars, whereas the hypoconid maintains a similar location.

The hypoconulid is not reduced. The highest cusp is the protoconid, followed by the metaconid. Paraconid, entoconid and hypoconid are of a similar size and slightly shorter than the metaconid. There is no lingual cingulum at the trigonid.

Humera : Complete humera of *H. minor* nov. sp. are absent in Carrascosa, only six distal epiphyses are available. The styloid process, present in only two specimens, is short and rounded. The condylus is large and both the trochlea and epicondylus are short. The fossa, as well as the furrows separating the condylus from the trochlea and from the epitrochlea, are shallow. This fact may have been accentuated by alteration, which might have affected the epitrochlea too, which is more rounded than in other species of *Pseudorhinolophus*.

Discussion - Two genera within the Rhinolophoidea, *Rhinolophus* and *Hipposideros*, present very similar dental morphologies. However, the absence of labial cingulum on the upper canine as well as the absence of P_3 indicates this material belongs to *Hipposideros*. The genus *Hipposideros* includes three subgenera with fossil representatives, *Pseudorhinolophus* SCHLOSSER 1887, *Brachipposideros* SIGÉ 1968, and *Syndesmotis* PETERS 1871. *Pseudorhinolophus* is characterized by one-cusped canines in the maxillae and a coronoid process higher than the M_1 -M_2 length of the mandible. *Brachipposideros* and *Syndesmotis* present two-cusped upper canines and a relatively shorter coronoid process. Even though no there are no complete mandibles in Carrascosa, the one-cusped upper canines of the material described above, indicates it belongs to *Pseudorhinolophus*.

The teeth of *Hipposideros (Ps.) minor* nov. sp. present certain morphological differences with the other species of *Pseudorhinolophus*. *Hipposideros (Ps.) egerkingensis* (REVILLIOD, 1922) is only known from its type locality, Egerkingen, Switzerland (upper Eocene), and is represented by an uncomplete mandible and maxilla. The fact that no more material from this species has been described up to now makes it practically impossible to compare with *Hipposideros (Ps.) minor* nov. sp. Three subspecies of this subgenus occur in several localities of Quercy in France, ranging from the Upper Eocene to the lower Oligocene (Remy *et al.*, 1987), *Hipposideros (Ps.)* cf. *morloti, Hipposideros (Ps.) schlosseri* (REVILLIOD) and *Hipposideros (Ps.) trassounius* SIGÉ. *H. morloti* (PICTET, 1855) resembles *H. minor* nov. sp. in size. However, the material described by Revilliod (1917) within this species is of very heterogeneous nature and without systematic validity (Sigé, pers. comm.). Therefore, comparisons have to be restricted to the holotype. This one, figured in Revilliod (1917, p. 11) is a lower right mandible carrying P_4M_1 M_2 and M_3, and shows important differences with the morphology of the mandible of *H. minor* nov. sp.. In

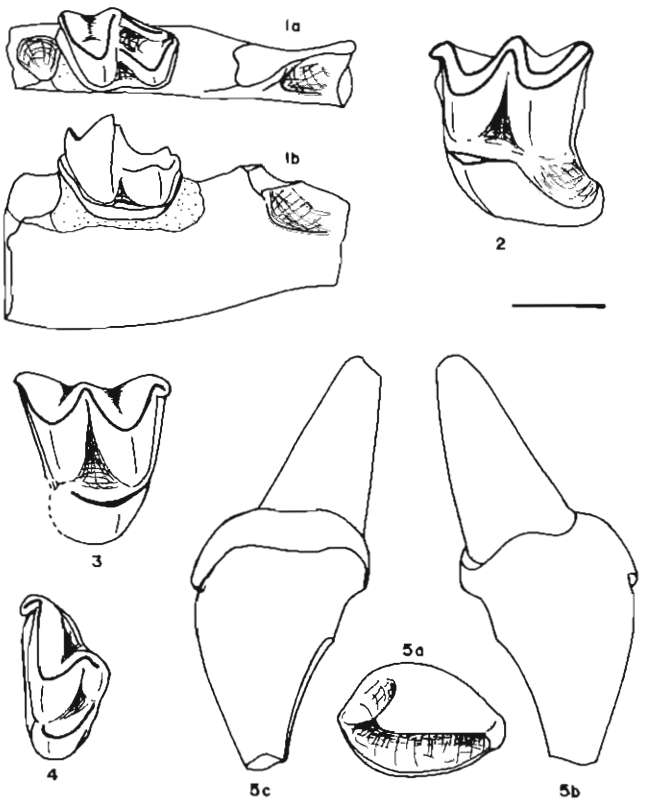

Figure 9 - ***Hipposideros (Pseudorhinolophus) minor*** nov. sp. **1** : fragment of left mandible with M_3 (CAS-283-Q). *Fragment de mandibule gauche avec M3 (CAS-283-Q).*

Hipposideros (Pseudorhinolophus) conquensis nov. sp. **2** ; holotype, left M^1 (CAS-8-Q). **3** : right M^2 (CAS-10-Q). **4** : left M^3 (CAS-13-Q). **5** : right upper canine (CAS-387-Q). (**a** : occlusal ; **b** : labial ; **c** : lingual ; **d** : distal ; **e** : mesial. The scale = 1 mm).
2 : Holotype, M^1 gauche (CAS-8-Q). 3 : M^2 droite (CAS-10-Q). 4 : M^3 gauche (CAS-13-Q). 5 : canine supérieure droite (CAS-387-Q). (a : occlusale ; b : labiale ; c : linguale ; d : distale ; e : mésiale. Echelle = 1 mm).

H. morloti, the height of the mandible increases gradually from the front towards the M_3. Just behind M_3, the mandible presents its maximal height, whereas in *H. minor* the height of the mandible is constant from P_2 to just behind M_2, where the base of the mandible bends dorsally (see fig. 9 : 16). Moreover, the symphysis in *H. minor* nov. sp. presents a ventral projection which is not observed in Revilliod's figure of *H. morloti*.

Another species, *H. schlosseri* (REVILLIOD, 1917), was imprecisely described by its author. This led Sigé to propose a lectotype for it within the original material, as well as a reference population, the population of the upper Eocene French locality of St. Néboule (Sigé 1978). Another well-documented population of *H. schlosseri* is described from the French late Eocene locality of Le Bretou (Sigé 1988). The comparison with these two populations shows that *H. schlosseri* is of larger size than *H. minor*. The postprotocrista of the M^{1-2}, in *H. minor* is directed less labially than in *H.schlosseri*

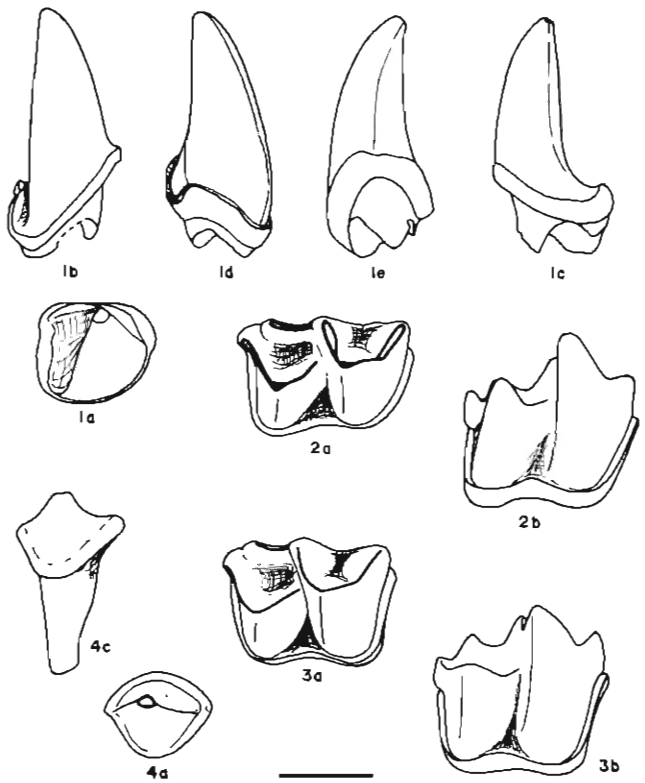

Figure 10 - ***Hipposideros (Pseudorhinolophus) conquensis*** nov. sp. **1** : right lower canine (CAS-7-Q). **2** : right M_1 (CAS-17-Q). **3** : right M_2 (CAS-19-Q). **4** : right P_2 (CAS-27-Q). (**a** : occlusal ; **b** : labial ; **c** : lingual ; **d** : distal ; **e** : mesial. The scale = 1 mm.

1 : Canine inférieure droite (CAS-7-Q). 2 : M_1 droite (CAS-17-Q). 3 : M_2 droite (CAS-19-Q). 4 : P_2 droite (CAS-27-Q). (a : occlusale ; b : labiale ; c : linguale ; d :distale ; e : mésiale. Echelle = 1 mm).

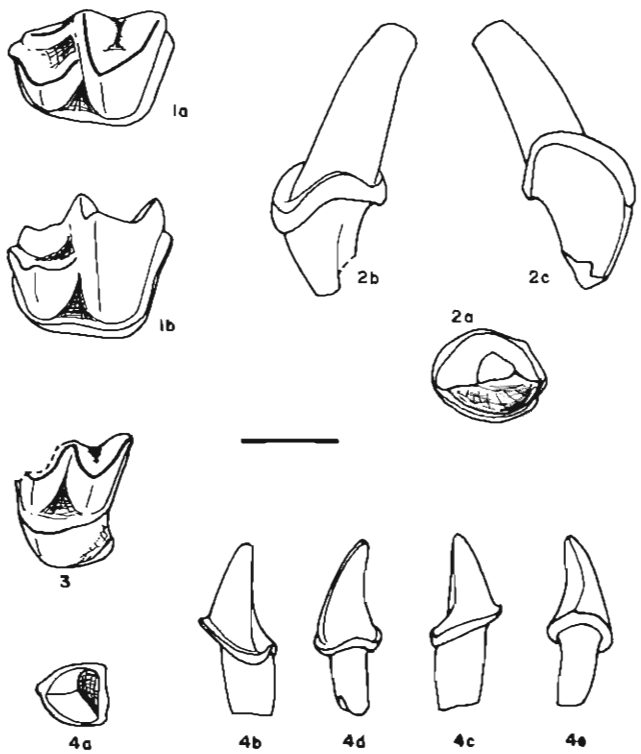

Figure 11 - ***Hipposideros (Pseudorhinolophus) conquensis*** nov. sp. **1** : right *(droite)* M_3 (CAS-21-Q).

Rhinolophus sp. **2** : left upper canine (CAS-69-Q). **3** : left M^2 (CAS-439-Q). **4** : left lower canine (CAS-351-Q). (**a** : occlusal ; **b** : labial ; **c** : lingual ; **d** : distal ; **e** : mesial. The scale = 1 mm).
2 : Canine supérieure gauche (CAS-69-Q). 3 : M^2 gauche (CAS-439-Q). 4 : canine inférieure gauche (CAS-351-Q). (a : occlusale ; b : labiale ; c : linguale ; d : distale ; e : mésiale. Echelle = 1 mm).

As a consequence, the protofossa is wider in the former species. The degree of distal reduction of the M^3 in both species is similar. However, in *H. minor*, the preprotocrista starts at the base of the paracone instead of being connected with the mesial cingulum as observed in *H. schlosseri*. The morphology of the lower teeth in both species is very similar, though the distal heel of the P_4, as well as the talonids of the lower molars seem slightly longer in *H. minor* nov. sp. A similar difference is observed in the mandible as that mentioned for *H. morloti*. In *H. schlosseri* the height of the mandible increases gradually in distal direction starting below the P_4 towards M_3 (see Revilliod 1917, p. 11 ; Sigé 1988, p. 91, fig. 25b and c).

A third species has recently been described from the French upper Eocene locality of Le Bretou, *Hipposideros (Ps.) trassounius* SIGÉ, 1988. This is a very small species, smaller than the new one, in which the upper teeth present shorter heels than in *H. minor* nov. sp., but with a thicker cingulum and a stronger parastyle. The postprotocrista of the M^{1-2}. Is shorter and distally directed. The P_4 is more slender than in *H. minor*, nov. sp. and reminds vaguely the P_4 *Rhinolophus*. In the M_1, the trigonid is narrower and the talonid proportionatelly shorter than in *H. minor* nov. sp.

Another species of *Pseudorhinolophus* is found in the Miocene localities of Bouzigues and Port-la-Nouvelle (France), *H. (Ps.) bouziguensis* SIGÉ. This species is considerably larger than *H. minor,* and presents numerous differences in the morphology of the teeth. The upper canine of the Miocene species presents a different wear pattern, which does not affect the whole of the distal edge, as it stops at a distance from the cingulum. The unworn part of the distal edge forms a distinct angle, observable in lateral view, which is not present neither in *H. minor* nov. sp. or in the other Oligocene species of *Pseudorhinolophus*. The upper molars present a free mesial cingulum which ends at the base of the protocone and which rarely joins the preprotocrista. Generally the preprotocrista ends at the internal base of the paracone. The M^3 of this species is more reduced, as the premetacrista is rudimentary or even absent in some cases. In the P_2 the height of the crown is taller at the labial side than at the lingual one.

HIPPOSIDEROS (PSEUDORHINOLOPHUS) CONQUENSIS NOV. SP.

Holotype - right M^1, number CAS-008-Q (fig. 9 : 2)

Hypodigm - Isolated teeth CAS-007, -010, -013, -017, -019, -021, -027, -387. (fig. 9 : 3-5 ; fig. 10 : 1-4 ; fig. 11 : 1)

Type locality - Carrascosa del Campo (province of Cuenca, Spain).

Distribution - MP25, upper Oligocene, Central Spain.

Diagnosis - Middle sized *Pseudorhinolophus*. Third upper molar with a strong distal reduction, the premetacrista less than half the length of the postparacrista. Height of the crown of P_2 at the labial side larger than at the lingual side. Talonid of the M_3 reduced both in length and in width.

Differential diagnosis - Similar in size to *H. (Ps.) schlosseri* (REVILLIOD), larger than *H. (Ps.) morloti* (PICTET) and *H. (Ps.) bouziguensis* SIGÉ. In the upper canine the wear at the distal edge does not reach the cingulum as in *H. morloti* and *H. minor* nov. sp. The mesial cingulum of the M^3 is not connected to the preprotocrista as in *H. schlosseri* and *H. morloti*. The premetacrista of the M^3 is shorter than in *H. minor* and longer than in *H. bouziguensis*.

Measurements - see Table 2.

Derivatio nominis - After the province of Cuenca, where the type locality is situated.

Material - 4 upper canines ; $2M^1$; $1M^2$; $5M^3$; 2 lower canines ; $2P_2$; $6M_1$; $3M_2$; $4M_3$.

Description - Upper canine : Long and rather narrow. At the lingual face it presents a well-developed cingulum, rather thick at the front and becoming narrower towards the distal part of the tooth. No clessar cingulum can be seen at the labial side. Tooth wear affects the posterior edge of the canine up to a short distance from the cingulum with the unworn edge, forming a distinct angle which can be seen in lateral view.

M^1 : the outline in occlusal view is subquadrate. At the disto-lingual side it presents a well-developed talon with a strong cingulum and without hypocone. The proximal cingulum is connected with the preprotocrista. At the end of the postprotocrista there is a ridge, which connects with the beginning of the cingulum of the talon. The distal cingulum ends at the base of the metacone and is not connected with either the postprotocrista nor with the talon cingulum.

M^2 : only one broken specimen of this element is available. The talon is missing, and there is no sign of a ridge parting from the postprotocrista towards the cingulum of the talon as in the M^1. The postprotocrista is bent towards the base of the metacone and ends without joining the distal cingulum. The talon is missing, but seems to have been considerably smaller than in M^1. The rest of the characters are as in the M^1.

		n	$\bar{x}$	min. - max.
M_1	L	4	1,84	1,82 - 1,88
	W_1	3	1,06	1,05 - 1,09
	W	3	1,11	1,09 - 1,17
M_2	L	2	1,88	1,84 - 1,92
	W_1	2	1,21	1,17 - 1,25
	W_2		1,19	1,13 - 1,29
M_3	L	5	1,64	1,60 - 1,68
	W_1	5	1,06	0,94 - 1,17
	W_2	5	0,76	0,60 - 0,82

		n	$\bar{x}$	min. - max.
C^*	L	4	1,99	1,92 - 2,00
	W	4	1,25	-
M^1	L	1	1,82	-
	W	1	2,58	-
M^3	L	5	1,19	1,17 - 1,25
	W	5	1,81	1,76 - 1,84
C_*	L	1	1,17	-
	W	1	1,13	-
P_2	L	2	1,17	1,13 - 1,21
	W	2	0,91	0.90 - 0.92

M^3 : the posterior part of this tooth is strongly reduced. Both metacone and metastyle are absent and the strongly reduced premetacrista measures about one third of the length of the preparacrista. The postparacrista is somewhat reduced, and it measures about one thirds of the length of the preparacrista. An independent anterior cingulum is present, ending at the mesial base of the protocone, not joining the preprotocrista, and leaning on the base of the paracone. No distal cingulum is present.

Lower canine : the cusp is tall, slender in lateral view and wide seen from the front. The occlusal outline is triangular and the tooth is surrounded by a continuous cingulum. The cingulum is thickest at the distal side ; labially it is considerably thinner than at its lingual side. A slisgt thickening of the cingulum can be observed at its lingual side.

P_2 : oval-shaped outline, with one root. The cusp is displaced towards the front and lingual margin of the tooth. A continuous cingulum is present, somewhat wider at the anterior angle ; at the labial side, the cingulum has a more gentle outline. The height of the crown at the lingual side is about two thirds of the height at the labial side.

M_1 : the trigonid is somewhat narrower than the talonid. In occlusal view, the paraconid, metaconid and entoconid are in line, whereas the hypoconulid has a more labial position. The entocristid is straight. The metaconid is the tallest of the lingual cusps, the paraconid and entoconid are similar in height, and the hypoconulid is the smallest one. The height of the hypoconid is approximately the same as that of the entoconid. At the trigonid, a very small lingual cingulum is present. The labial cingulum is well developed and uniformly thick.

M_2 : The morphology of this element corresponds more or less to that of the M_1. It has, however, a wider trigonid, which is as wide as the talonid. Moreover, there is no lingual cingulum at the trigonid.

M_3 : the talonid is only slightly reduced, as the entoconid is situated more labially than the paraconid and the metaconid. The hypoconid has a similar relative position as in M_1. The entocristid forms a slight bend near its contact with the metaconid. The height of the entoconid and hypoconid is reduced. The hypoconulid is not reduced and stands independent and as wide apart from the entoconid as in the M_1 and M_2.

Discussion - *Hipposideros (Ps.) conquensis* nov. sp. resembles *H. schlosseri* (REVILLIOD) strongly, both in size and morphology. Nevertheless, several important differences are observed when we compare *H. conquensis* nov. sp. with the Upper Eocene populations of *H. schlosseri* from Le Bretou and St. Néboule. The upper canines of *H. conquensis* are very similar to those of the reference locality, St. Neboule (Sigé 1978): the lingual cingulum presents the same morphology; and a distinct angle is observed on the distal edge of the upper canine of Plate 1, similar to that described in the upper canines of *H. conquensis* nov. sp. However, this angle is not observed in either Revilliod (1917, p. 18, fig. 11), nor in the population from Le Bretou (Sigé 1988, p. 91, fig. 26a and b). In the latter population the lingual cingulum of the upper canines is also quite different from that observed in *H. schlosseri* from St. Néboule or in *H. conquensis* nov. sp.

In the M^1 of *H. schlosseri* of either St. Néboule or Le Bretou, the postprotocrista runs towards the base of the metacone, where it ends. Instead, in *H. conquensis* nov. sp., the postprotocrista is distally directed and connects with the talon cingulum with a ridge, absent in the former species, in which the cingulum of the talon starts at the lingual base of the protocone.

Two further differences can be observed in the M^3 both species. In *H. conquensis* nov. sp. this tooth is shorter, due to a stronger reduction of the premetacrista than what is observed in *H. schlosseri*. Another difference lies on the preprotocrista, which starts at the base of the paracone in *H. conquensis* nov. sp. instead of being connected to the mesial cingulum as in *H. schlosseri*.

The two species present a very similar morphology in the lower teeth, except for the P_2, which has a different height at the labial and lingual sides in *H. conquensis*.

H. conquensis nov. sp. is larger than the other species of *Pseudorhinolophus* described in the upper Eocene and lower Oligocene, *H. morloti* and *H. trassounius*. It is also larger than the other species from Carrascosa, *H. minor*. *H. conquensis* nov. sp. differs from these smaller species in the wear pattern of the distal edge of the upper canine, the morphology of the talon of the M^1, and in the degree of distal reduction in the M^3, which is more intense in *H conquensis* nov. sp.

In the lower Miocene localities of Bouzigues (Sigé 1968) and Port-la-Nouvelle (Legendre 1980), another species of *Pseudorhinolophus* is represented, *Hipposideros (Ps.) bouziguensis* SIGÉ. This species is larger than *H. conquensis* nov sp., but presents interesting similarities with it in the characters that separate *H. conquensis* nov. sp. with *H. schlosseri*. The upper canine of *H. bouziguensis* presents the distal lateral angle observed in *H. conquensis* nov. sp. In certain upper molars from the locality of Bouzigues and in all from Port-la-Nouvelle, the mesial cingulum is isolated and the preprotocrista starts at the lingual base of the pa-

racone. This morphology is also found in the M^3 of *H. conquensis* nov. sp. On the other hand, this new-species presents a less reduced M^3 than in the Miocene species.

Family RHINOLOPHIDAE Bell, 1836
Genus *Rhinolophus* LACEPEDE, 1799

RHINOLOPHUS SP. (fig. 11 : 2-4)

Measurements - see Table 3.

		n	x̄	min. - max.
M_1	L	1	1,78	-
	W	1	0,80	-
	W	1	0,94	-
M_3	L	2	1,58	1,56 - 1,60
	W	1	1,01	-
	W	2	0,64	0,58 - 0,70

		n	x̄	min. - max.
P^4	L	1	1,56	-
	W	1	0,86	-
M^1	L	1	(1,56)	-
	W	1	2,00	-
M^3	L	1	1,17	-
	W	1	1,96	-
P_2	L	2	1,19	1,17 - 1,21
	W	2	0,62	-

Material - 2 upper canines, 1 M^2, 1 lower canine.

Description - **Upper canine** : Oval outline in occlusal view. The cingulum is continuous and well developed. At the labial side it has the typical sinuous pattern of *Rhinolophus* species. At the lingual side the crown presents its maximum height and its lowest at the mesial side. The tooth wear affects only the tip of the cusp. The root is strong and rounded and it forms an angle with the crown.

M^2 : there is only one broken specimen of this element; the parastyle and most part of the preparacrista are absent. There is a small disto-lingual talon. The cingulum of the talon is isolated, as the mesial cingulum joins the preprotocrista and the postprotocrista joins the distal cingulum.

Lower canine : the only specimen presents a triangular outline in occlusal view. The cingulum, continuous all around the base of the tooth, is slightly widened at its most mesial point. The root is longer than wide.

Discussion - Several species of fossil *Rhinolophus* are known from the Oligocene and Miocene of Europe. These might be divided into three groups on the basis of size and morphology, and relating them to the recent species of this genus. In this way, *R. delphinensis* GAILLARD, *R. cluzeli* HUGUENEY, *R. lemanensis* REVILLIOD, and *R. csakvarensis* KRETZOI belong to the *R. ferrumequinum* group ; *R. grivensis* (DEPERET) and *R. lissiensis* MEIN to the *R. euryale* group and *R. priscus* REVILLIOD to the *R. hipposideros* group. *Rhinolophus* sp. from Carrascosa clearly belongs to this last group, though it is somewhat larger than the recent *R. hipposideros*.

Rhinolophus priscus was described by Revilliod from a heterogeneous material coming from Quercy and Mormont (cf. Sigé, 1978). As no holotype was formally established among this material, the authors have described as *Rhinolophus* cf. *priscus* material from different upper Eocene and lower Oligocene localities of Quercy that might fit with *R priscus* (see Remy *et al.* 1987). No upper nor lower canines of *R. priscus* were described by Revilliod (1920). The only other element present in Carrascosa, the M^2, seems to have smaller talon than in the M^2 of the material described by Revilliod.

The lingual morphology of the upper canine of *Rhinolophus* sp. from Carrascosa is very similar to that of the upper canines of *Rhinolophus* cf. *priscus* from St. Néboule (Sigé, 1978). However, the size of these teeth in the French population is larger. *Rhinolophus* sp. from Carrascosa seems therefore to belong to a species of smaller size than *R. priscus*.

Several important differences can be observed between recent *R. hipposideros* (BECHSTEIN) and *Rhinolophus* sp. from Carrascosa. In the upper canine, the base of the root in the recent species is much stronger;

the lingual cingulum of this tooth forms a U and passes gradually from thicker at the mesial edge to thinner at the distal edge. In *Rhinolophus* sp. the lingual cingulum has the form of an asymmetrical V, being the two proximal thirds of its length thick passing abruptly to thin at the distal third. In the M^2 of *R. hipposideros* the lingual half of the crown is narrower than the labial half because of a distal constriction present at a short distance after the point where the postprotocrista joins the distal cingulum. The lower canine is very similar in both species, though the occlusal widening of the mesial cingulum in *Rhinolophus* sp, is slightly displaced towards the lingual side of the crown in *R. hipposideros.*

Family MEGADERMATIDAE Allen, 1864
Genus *Megaderma* GEOFFROY, 1810

MEGADERMA LOPEZAE NOV. SP.

Holotype - left first upper molar, CAS-395. (fig. 12 : 2).

Hypogim - isolated teeth, CAS-24, -202, -335, -342, -470 (fig. 12 : 1,3-6).

Type locality - Carrascosa del Campo (province of Cuenca, Spain).

Distribution - MP5, upper Oligocene, Central Spain.

Diagnosis - Small sized *Megaderma.* Small talon in P^4 and M^1. Wide trigonid in M_1, talonid of M_3 with entoconid, hypoconid and hypoconulid as well as a short entocristid.

Differential diagnosis - Smaller than recent *Megaderma spasma* (LINNAEUS) and slightly smaller than *H. jaegeri* SIGÉ. Talonid of M_3 less reduced than in *M. vireti* MEIN and *M. spasma.* Cingulum in lower molars thinner than in *M. jaegeri.* Talon of upper molars wider and shorter than in *M. spasma* : postparacrista in M^3 more reduced than in *M. spasma.*

Measurements - see Table 4.

		n	$\bar{x}$	min. - max.
C•	L	2	1,17	-
	W	2	0,97	0,94 - 1,17
C.	L	1	0,66	-
	W	1	0,70	-

Tableau 4 - Measurements in mm of the teeth of ***Megaderma lopezae*** nov. sp. from Carrascosa del Campo.

*Mesures en mm des dents de **Megaderma lopezae** nov. sp. de Carrascosa del Campo.*

Derivatio nominis - dedicated to the Spanish vertebrate paleontologist, Dr. N. López-Martínez (Madrid).

Material - $1P^4$, $1M^1$, $2M^3$, $1M_1$, $2M_3$.

Description - P^4 : the occlusal outline of this tooth is trapezoidal. At the lingual margin it presents a short and narrow talon. Only one cusp is present, located at the centre of the crown. At the lingual side there is a continuous and strong cingulum. This cingulum is connected distally with the labial cingulum. At the middle of the labial side, the labial cingulum ends. There is a small isolated cingulum at the first half of the labial side, which does not reach the mesial apex of the tooth.

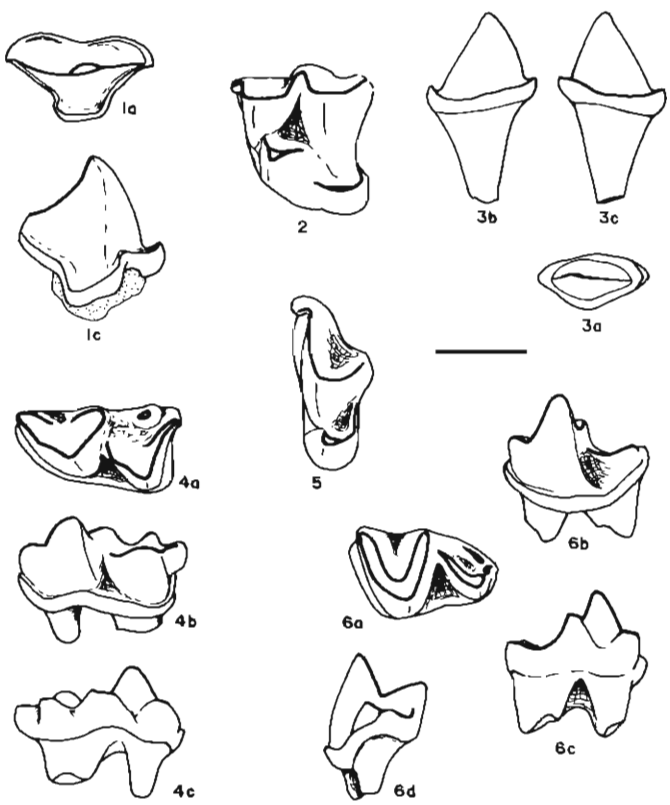

Figure 12 - ***Megaderma lopezae*** nov. sp. **1** : right P^4 (CAS-470-Q). **2** : holotype, left M^1 (CAS-395-Q). **3** : right P_2 (CAS-24-Q). **4** : left M_1 (CAS-202-Q). **5** : left M^3 (CAS-342-Q). **6** : left M_3 (CAS-335-Q). (**a** : occlusal ; **b** : labial ; **c** : lingual ; **d** : distal ; **e** : mesial. The scale = 1 mm).

1 : P^4 droite (CAS-470-Q). 2 : holotype, M^1 gauche (CAS-395-Q). 3 : P_2 droite (CAS-24-Q). 4 : M_1 gauche (CAS-202-Q). 5 : M^3 gauche (CAS-342-Q). 6 : M_3 gauche (CAS-335-Q). (a : occlusale ; b : labiale ; c : linguale ; d : distale ; e : mésiale. Echelle = 1 mm.

M^1 : this tooth is represented by a single specimen with a broken metastyle. It presents a massive look with a well-developed ectoloph, the mesostyle projecting labially. The postparacrista and the premetacrista are not reduced. The metacone is the largest cusp. The

protocone stands quite close to the paracone and the end of the short preprotocrista leans on its postero-lingual base. The short postprotocrista ends near the short and narrow valley that separates the protocone from the metacone. A strong but short talon is present, provided of a very thick cingulum. At the mesial side there is a narrow cingulum which runs down to reach nearly the lingual base of the protocone. Distal and labial cingula are absent.

M^3 : this short and wide tooth presents a strong distal reduction. The postparacrista is reduced, and has a length of about two thirds the length of the preparacrista. There is no metacone and the premetacrista is completely absent. The small protocone has no preprotocrista and it leans directly on the base of the paracone. The postprotocrista is long ; first it runs distally and then turns towards the mesostyle. There is a long mesial cingulum which runs from the base of the well-developed parastyle to the mesial base of the protocone. No other cingulum is present.

P_2 : this element is long and narrow, and it consists of one flat cusp which is slightly displaced towards the front of the tooth. The root is also long and narrow. The base of the crown is surrounded by a strong and continuous cingulum.

M_1 : this tooth is nyctalodont and relatively elongated. The trigonid is narrow, and the paraconid stands wide apart from the metaconid. The entocristid is absent. The well-developed hypoconulid stands wide apart from the hypoconid. The mesial root is smaller than the distal root. The only available specimen is highly worn, but in spite of this, it is evident that the hypoconid is the second cusp in height after the protoconid. The paraconid and metaconid are of similar height, and the hypoconulid is slightly shorter but stronger at its base, than the entoconid. The cingulum is moderately wide and is concave in lateral view at the base of the protoconid. There is no lingual cingulum.

M_3 : the trigonid of this tooth is well developed and the width of the talonid strongly reduced. The entoconid, hypoconid and hypoconulid stand apart, without any crista joining them. A weak and short crista runs from the entoconid in the direction of the metaconid, but stops at half way distance between the two cusps. The paraconid is shorter than the metaconid. The cingulum is as strong as in M_1. In labial view, at the end of the trigonid, it ascends upwards towards the top of the hypoconulid.

Discussion - *Megaderma lopezae* nov. sp. is a small *Megaderma* species, and it is of smaller size than recent *Megaderma spasma* (LINNAEUS). It is the smallest species of the genus described up to now.

The oldest representative of the Megadermatids in Europe is *Necromantis adichaster* WEITHOFER, 1897, known from the French upper Eocene and Oligocene of Quercy (Remy *et al.* 1987). This species differs strongly both in size amd in morphology with the material of Carrascosa. It is larger, and presents well-developed talons in P^4, M^1 and M^2, and the lower molars present no reduction in the talonid cusps, and no transverse compression of the trigonids.

In the Oligocene French locality of St. Victor-la-Coste, remains of *Megaderma* sp. of large size have been described (Sigé 1967). Unfortunately, it consists only of a toothless mandible and consequently comparison with *M. lopezae* nov. sp. is not possible.

In the Miocene this genus is more abundant, and four different species are known from France and Central Europe. All of them are quite larger than the new species. *M. brailloni* SIGÉ, 1968 is known from the lower Miocene localities of Bouzigues (Sigé 1968) and Serre de Verges (Meurisse *et al* 1969), *M. gaillardi* (TROUESSART, 1898) from the middle Miocene localities of La Grive St.-Alban (Guérin & Mein 1971) and Escobosa (Sesé 1986), *H. vireti* MEIN, 1964, from La Grive St.-Alban and the upper Miocene localities of Lissieu (Mein 1964) and Kohfidisch (Bachmayer & Wilson 1970) and *M. lugdunensis* (DEPERET, 1892) known from the lower Miocene locality of Vieux Collonges (Guérin & Mein 1971), middle Miocene of Neudorf (Zapfe 1950) and upper Miocene of Lissieu. In these four species the ectoloph is strongly modified, the post paracrista and premetacrista are reduced, and the mesostyle stands at a more lingual position than the parastyle and the metastyle. *Megaderma gaillardi* presents a stronger mesial cingulum in the upper molars than what is observed in *M. lopezae*. Both the former species and *M. lugdunensis* present an expansion at the distal margin of the M^3 between the paracone and the metacone. This feature is absent in *M. lopezae* nov. sp. *M. brailloni* SIGÉ, more than twice the size of the species from Carrascosa, presents a very large talon in the M^{1-2}.

Another species of *Megaderma* (*M. jaegeri* SIGÉ, 1976) has been described from the Miocene locality of Beni Mellal (Morrocco). The size of this species is smaller than that of the European species, but slightly larger than *Megaderma lopezae* nov. sp. In the upper molars there is no mesial cingulum and the talon is much larger than in the Spanish species. In the lower molars, the cusps present a similar location, but the entoconid is shorter than the hypoconulid, and the cingulum is thicker. The postcristid makes a similar bend at the half of its length as that of the new species. This feature is not present in the other species of *Megaderma*.

In the middle Miocene locality of Riversleigh in Australia, two different species of Megadermatids have

been described. *Macroderma godthelpi* HAND, 1985, and another unnamed species. *M. lopezae* differs strongely from *M. godthelpi.* The Australian speçies is larger. It presents in its upper molars distal cingulum, larger talons and no parastyle. They differ too in the relative size of the cristas that form the ectoloph. In the lower teeth, the degree of transverse compression of the trigonid of the M_1 of *M. godthelpi* is lower than in *M. lopezae* nov. sp. and the inflexion of the labial cingulum occurs between the trigonid and the talonid, instead of below the protoconid. Further differences are observed in the M_3, which presents no distal cingulum and a larger talon.

From the Pliocene of Europe, two other species of Megaderma are known. *M. janossyi* TOPAL (1974), from the Pliocene of Hungary, is known only from a mandibular fragment with a broken M_1. It is of larger size than *M. lopezae* nov. sp. and presents a thicker cingulum. The Late Pliocene species *M. mediterraneum* SIGÉ (1974) from southern France is also larger. No M_1 are known from *M. mediterraneum*, so no direct comparison with the M_1 of *M. lopezae* nov. sp. is possible. However, considering the position of the entoconid and hypoconulid in the M_2 of *M. mediterraneum*, these two cusps must have stood less separate in the M_1 of *M. mediterraneum* than in the new species.

When compared to recent Megadermatids, *M lopezae* nov. sp. most resembles *Megaderma spasma* and *Cardiaderma cor.* It shares with *C. cor* the labial situation of the mesostyle of M^1, the shape of the M^3 and the absence of labial cingula in the upper molars. On the other hand, it differs strongly in the shape of the protocone and talons of the upper molars. *M. spasma* presents also larger talons than *M. lopezae* nov. sp., but presents parastyle in the upper molars, postprotocrista in the M^3, and the P^4 of of this species is the one that most resembles the P^4 of *M. lopezae* nov. sp.

COMMENTS ON THE PHYLOGENETIC RELATIONSHIPS OF THE CHIROPTERA OF CARRASCOSA.

The absence of a good documentation of fossil Tertiary bats in Spain does not permit us to establish phylosenetic relationships of the species described from Carrascosa with other European Tertiary bats. Considering the slight differences observed between them, it is possible that *Hipposideros (Ps.) minor* nov. sp. might be related to *Hipposideros (Ps.) morloti* (PICTET) and *Hipposideros (Ps.) conquensis* nov. sp. with *Hipposideros (Ps) schlosseri* (REVILLIOD). From this point of view, it might be considered that the characters that differenciate the above-mentioned species of *Hipposideros* are in a more evolved state in the species from Carrascosa, especially those that are found is the same or an even more advanced state in the Miocene species *Hipposideros (Ps.) bouziguensis*, the last known representative of the subgenus *Pseudorhinolophus.*

Within the three lineages of fossil *Megaderma* proposed by Sigé (1976), *M. lopezae* nov. sp. would fit, considering the size, in the third group, together with the Miocene species *M. jaegeri* SIGÉ, and might even be questioned as a possible ancestor for this species, on the basis of the more evolved characters found in *M. jaegeri* : deformed ectoloph, absent mesial cingulum and large talon in first upper molars, reduced entoconid in M_1. Unfortunately, no M^3 are known from this species, a character that might be definite to establish this relationship, in the same way that it excludes the phylogenetic relationship of *M. lopezae* nov. sp. with recent *M. spasma*, which presents third upper molars less reduced distally.

More recently, in Hand (1985), the phylogenetic relationships bebween recent and fossil Megadermatids has been analysed. According to the polarity of characters established by Hand in this paper, *Megaderma lopezae* nov. sp. presents a majority of primitive characters, and would stand at the base of the cladogram proposed in this paper. The primitive characters present in *Megaderma lopezae* are small size, short talons in P^4, M^1 and M^2, the presence of parastyle in M^1, a moderate transverse compression of the trigonid in M_1 the presence of entoconid, hypoconid and a small entocristid in M_3. Certain characters that might help to relate *M. lopezae* nov. sp. with other Megadermatidae, such as the number of cusps in the upper canine, the loss of P^2 and relative size of the lower molars are lacking in our material.

COMMENTS ON THE ORIGIN OF THE FOSSIL ASSOCIATION OF CARRASCOSA.

The distribution of the recent species of *Hipposideros* is restricted to the tropical regions of the Old World, as well as to some subtropical regions. They can either be found living in caves, frequently forming large colonies, or occasionally living in trees, and found as solitary individuals (Hill & Smith 1984). The genus *Rhinolophus* presents a similar but wider distribution, as some species can be found in the temperate regions of Europe. The species of this genus can also roost both in trees and in caves, the large colonies being found in caves. *Megaderma*, relatively frequent in the Tertiary of Europe, is distributed in the present only in southeastern Asia, where it is found in trees and in caves, sometimes sharing this refuge with *Rhinolophus* and *Hipposideros.*

This sort of association is also frequently found in the

Tertiary of Europe, especially during the Miocene. For instance, in the Oligocene we find the three genera together in St.-Victor-la-Coste (France) ; in the Miocene in La Grive St. Alban, Serre de Verges and Vieux-Collonges in France, in Escobosa in Spain (Sesé 1986 ; the M^1 n.5 of figure 1 belongs to *Hipposideros*) and in Beni Mellal in Morrocco ; or in the Pliocene in Sète (France). However, all these localitises are karstic. In fluvio-lacustrine localities these three genera are not found together ; at the most, *Hipposideros* and *Rhinolophus* are found together, as in Coderet. These latter localities are in general poorer in bat remains, and the genera are generally representatives of the Molossidae and Vespertilionidae, although *Hipposideros, Rhinolophus* and *Megadarma* are not excluded. Therefore, considering the quantity of bat remains, the association of species and the low diversity they represent, Carrascosa del Campo is an unusual locality. Having in mind the paleoenvironment reconstructed for Carrascosa, it is difficult to imagine how such a large quantity of bat remains could have concentrated in the open air and preserved without being weathered. Practical observations show that small vertebrate bones are weathered very quickly and become destroyed unless they are rapidly buried (Behrensmeyer 1978). In caves, where bats concentrate in large numbers, the constant conditions of humidity and temperature help to preserve the bones of the animals that die there. This is the reason why in karstic localities bat remains are abundant and relatively well preserved. Considering the large quantity of bat remains in Carrascosa, as well as the fact that two or the genera present (*Hipposideros* and *Rhinolophus*) frequently form colonies in caves, occasionally associated with *Megaderma*, it is tempting to propose that the bat remains accumulated originally in a karst and were somehow transported afterwards and redeposited in the place from which they were excavated.

A similar interpretation has been given to the origin of the bat fauna of the Riversleigh Formation in Australia, a complex of lake-originated localities. The fossil bat remains of these localities have been interpreted as coming from nearby caves, the bones accumulated on the ground of these having been periodically flushed by streams into the pools and lakes, that are now the fossil deposits (Hand 1989). The higher diversity of bats found in Riversleigh (certain families absent in Carrascosa, such as Vespertilionids, Molossids and Emballonurids are represented in the Australian deposits), might be related to the fact that the Riversleigh Formation has been interpreted as originated in a rainforest, where the diversity of bat fauna is expected to be higher than in the warm, dry, little forested landscape of Carrascosa. The underlying mesozoic limestones, faulted before the formation of the locality, might have given place to an old karst, nowadays completely dismantled, where the Rhinolophoidea found in Carrascosa might have taken refuge (Diaz Molina, pers. comm.).

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